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Metrical analysis of growth changes in the jaws and teeth of normal, protein deficient and calorie deficient pigs

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INTRODUCTION

The pig is a useful animal for studying the effects of dietary deficiencies on the growth of jaws and teeth. Previous work, using the Large White strain, dealt with either the effects of general undernutrition (Tonge & McCance, 1965) or the more specific effects of calorie deficiency (Tonge & McCance, 1973). In the present study, the separate effects of protein and calorie deficient diets on the development and growth of the jaws and teeth of pigs during the first two years of life were assessed.

MATERIALS AND METHODS

Skulls were obtained from pigs subjected to protein and calorie deficient diets as well as from well-nourished pigs: details of their care, diets, general growth and behaviour have been published elsewhere (McCance & Widdowson, 1966; McCance, 1968; Widdowson, 1968). In brief, when piglets were about 10 days old and 3 kg in weight, they were separated into three groups. Control animals were allowed unlimited quantities of a mixture containing a proprietary pig food and cereal–fish meal with a total protein content of 19% by weight: at one year these animals weighed about 170 kg and at two years about 265 kg. The calorie deficient (CD) animals were rationed to 90 g per day of the same diet. They gained weight very slowly, reaching only 5–6 kg at one year and only about 10 kg at two years. The protein deficient (PD) animals were given the same diet as the CD pigs, plus unlimited calories in the form of sugar or fat: these animals weighed 10–14 kg at one year and about 23 kg at two years.

Five skulls were obtained from each of the control, PD and CD groups at one year, and a further five from each of the PD and CD groups at two years. Two control animals were killed at two years, and a number of skulls from well-fed pigs aged from 20–30 months was also studied. The skulls were cleaned, sectioned midsagittally, and each half skull was radiographed with its medial surface lying on the film, using a tube-film distance of 0·75 m. The parameters studied are shown in Figures 1 and 2. Measurements were made to the nearest 0·1 mm directly from the radiographs, using callipers fitted with a vernier scale. In general, parameters in the upper jaw were measured parallel to the occlusal plane of the erupted teeth, and those in the lower jaw parallel to its lower border. Overall length (*BC*) was measured to the anterior extremity of the alveolar process in both jaws. In the upper jaw, the posterior extremity was taken to be the point where the shadow of the lower border of the zygomatic arch crossed the posterior border of the medial pterygoid plate. In

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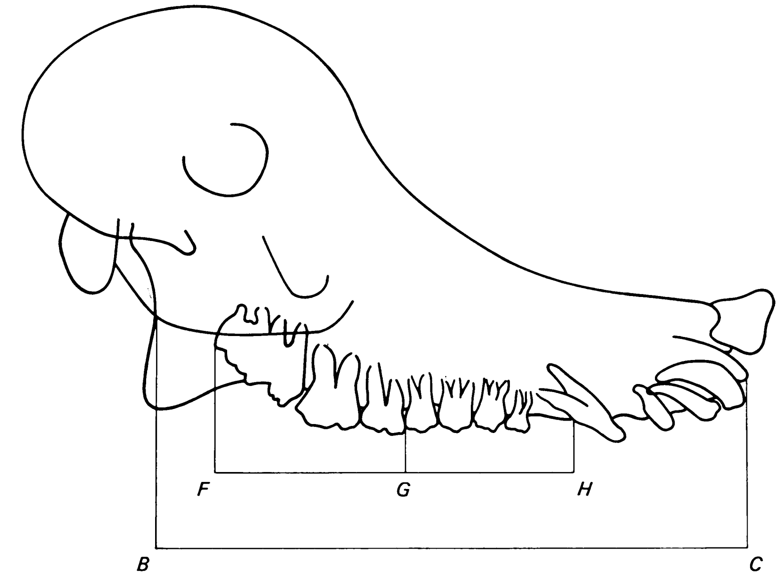

Fig. 1. Tracing of a radiograph of the skull and upper jaw of a two years old control pig showing the measurements used in the investigation.

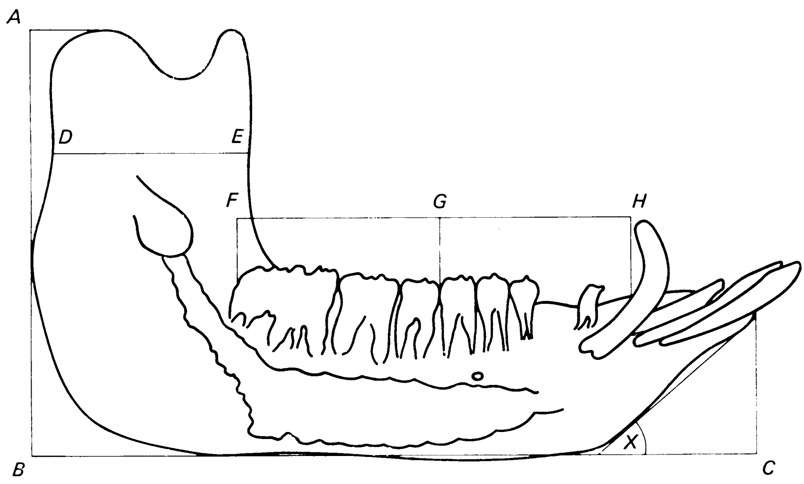

Fig. 2. Tracing of a radiograph of the mandible of a two years old control pig showing the measurements used in the investigation.

the lower jaw, the height of the ascending ramus (*AB*) was measured perpendicular to the lower border of the mandible, and its width (*DE*) was taken to be the shortest distance between the anterior and posterior borders. The degree of proclination of the lower labial alveolar process was measured as the angle *X* between a tangent to the anterior surface of the alveolar process and the line *BC*. All jaw measurements were taken from the right side.

The mesio-distal dimension of the crown of each molar tooth was measured from the radiographs: where a tooth is rotated in the jaw, the estimate will of course be less than the true size because such a tooth will not present its maximum mesio-distal length to the X-ray beam. An indication of contralateral asymmetry of molar crown diameter in the PD animals was obtained by dividing the difference in size of

Table 1. *Length and height of mandible (mm)*

Group	Number of animals	Length body (S.D.)	Height ramus (S.D.)	$\frac{\text{Length}}{\text{Height}}$ (S.D.)
Control 1 year	5	252 (14·6)	133 (3·4)	1·89 (0·07)[a, b]
PD 1 year	5	166 (11·9)	76 (5·6)	2·19 (0·08)[a, c]
CD 1 year	5	130 (5·8)	55 (2·2)	2·39 (0·07)[b, c]
Control 2 years	2	293	165	1·79
PD 2 years	5	216 (9·7)	97 (5·7)	2·23 (0·09)[d]
CD 2 years	5	161 (6·1)	70 (2·0)	2·31 (0·06)[d]

Differences a, a $P < 0{\cdot}01$; b, b $P < 0{\cdot}01$; c, c $P < 0{\cdot}01$; d, d $P > 0{\cdot}05$.

Table 2. *Height and anteroposterior width of ramus (mm)*

Group	Number of animals	Width (S.D.)	$\frac{\text{Height}}{\text{Width}}$ (S.D.)
Control 1 year	5	67·2 (5·9)	1·98 (0·13[a, b]
PD 1 year	5	41·3 (5·2)	1·84 (0·13)[a]
CD 1 year	5	35·7 (2·4)	1·54 (0·08)[b]
Control 2 years	4	76·0 (2·9)	2·19 (0·12)[c, d]
PD 2 years	5	51·9 (2·9)	1·87 (0·05)[c]
CD 2 years	5	40·1 (2·9)	1·74 (0·13)[d]

Differences a, a $P > 0{\cdot}05$; b, b $P < 0{\cdot}01$; c, c $P < 0{\cdot}01$; d, d $P < 0{\cdot}01$.

corresponding molar teeth from the left and right sides by the mean size of that type of molar tooth, the result being expressed as a percentage. The control group used for this purpose included animals aged from 1·0 to 2·5 years because, in the well-fed pig, the full crown size of all three molar teeth is established at one year. Calorie deficient pigs were not examined for molar asymmetry because of the occasional absence on one side or the other of a third permanent molar.

The length (*GH*) of the alveolar process occupied by the premolar teeth plus the post-canine diastema, was measured between points on the alveolar margin from the distal surface of the canine to the mesial surface of the first permanent molar. The extent of crowding of the molar teeth was assessed by dividing the distance (*FG*) of the space occupied by these teeth (from the mesial surface of M_1 to the distal surface of M_3) by the sum of the mesio-distal diameters of the molars.

RESULTS

Jaw measurements

The results are given in Tables 1–4. Table 1 shows that in the PD animals, and to a greater extent in the CD animals, the mandible was much shorter than in the controls. In addition, the ratio of the length of the body to the height of the ascending ramus was least in the control groups and greatest in the CD animals. Table 2 shows that ramal height was reduced proportionately more than ramal width in both groups of malnourished animals, and that, once again, the CD group was most affected. It is apparent from Table 3 that, over the two years period, the labial alveolar process of the mandible had become more proclined in both the PD and CD groups as compared with controls. The differences between the ratios of upper to lower jaw lengths in the experimental and control groups (Table 4) were not statistically significant.

Table 3. *Proclination of lower labial alveolus (degrees)*

Group	Number of animals	Angle of proclination (S.D.)
Control 1 year	5	33·7 (5·1)[a,b]
PD 1 year	5	26·3 (6·1)[a]
CD 1 year	4	22·8 (3·3)[b]
Control 2 years	10	40·3 (2·4)[c,d]
PD 2 years	5	23·1 (1·5)[c]
CD 2 years	5	20·4 (2·9)[d]

Differences a, a $P > 0{\cdot}05$; b, b $P > 0{\cdot}05$; c, c $P < 0{\cdot}001$; d, d $P < 0{\cdot}001$.

Table 4. *Upper and lower jaw lengths (mm)*

Group	Number of animals	Mandible (S.D.)	Upper jaw (S.D.)	$\frac{\text{Mandible}}{\text{Upper jaw}}$ (S.D.)
Control 1 year	5	252 (14·6)	219 (8·3)	1·16 (0·06)
PD 1 year	5	166 (11·9)	134 (10·0)	1·24 (0·02)
CD 1 year	5	130 (5·8)	107 (3·4)	1·21 (0·03)
Control 2 years	4	321 (47·9)	263 (13·1)	1·21 (0·19)
PD 2 years	5	216 (9·7)	173 (10·4)	1·24 (0·04)
CD 2 years	5	161 (6·1)	128 (5·1)	1·25 (0·05)

Table 5. *Mesio-distal size (mm) of mandibular molars*

Group	Number of teeth	M_1 (S.D.)	M_2 (S.D.)	M_3 (S.D.)
Control 1 year	8	17·9 (1·0)	23·2 (0·8)	36·9 (2·6)
PD 1 year	10	18·1 (0·5)	22·7 (0·9)	21·8 (8·1)
CD 1 year	8	17·7 (0·9)	20·3 (0·9)	5·3 (1·4)
Control 2 years	16	16·7 (1·1)	22·9 (1·6)	38·9 (3·5)
PD 2 years	10	18·1 (0·6)	22·1 (1·0)	32·2 (3·4)
CD 2 years	10	18·4 (0·6)	20·5 (1·2)	26·2 (2·7)

Tooth measurements

Tables 5 and 6 demonstrate that, in the PD and CD groups, the mean of the mesio-distal diameters of the first permanent molar crowns was similar to that of the control groups. The diameters of the second molars were only slightly diminished in the two experimental groups, but those of the crowns of the third permanent molars were dramatically reduced in both upper and lower jaws. In one year old CD pigs mandibular M_3 diameters were only 14 % of those of the corresponding teeth in one year old controls, although after two years they had reached 67 % of the control size. In the upper jaw of one year old CD pigs the third permanent molars were not visible radiographically, while after two years they had only achieved a crown dimension of 57 % that of the control animals.

Contralateral asymmetry of molar crown size in the PD pigs (Table 7) was greatest in M_3 and least in M_1. In the control animals, not only was asymmetry of M_1 greater than in the PD group, but, in the mandible, M_1 was more asymmetrical than either M_2 or M_3. The greatest contralateral asymmetry was found in M_3 of one year old PD pigs.

Table 6. *Mesio-distal size (mm) of maxillary molars*

Group	Number of teeth	M_1 (S.D.)	M_2 (S.D.)	M_3 (S.D.)
Control 1 year	8	18·6 (0·7)	24·1 (1·2)	36·1 (2·5)
PD 1 year	10	18·3 (0·2)	21·8 (1·3)	17·9 (4·3)
CD 1 year	9	17·8 (0·6)	18·7 (0·9)	No teeth present
Control 2 years	14	18·1 (1·4)	24·0 (0·9)	38·1 (2·2)
PD 2 years	10	18·7 (0·5)	22·6 (1·2)	31·0 (3·5)
CD 2 years	10	17·7 (1·3)	20·3 (3·1)	21·6 (4·5)

Table 7. *Contralateral molar asymmetry* $\left(\% \dfrac{\text{difference}}{\text{mean size}}\right)$

Group	Number of pairs	Mandible M_1	Mandible M_2	Mandible M_3
Control 16 months	24	4·9	1·9	4·0
PD 1 year	5	0·9	1·3	10·0
PD 2 years	5	2·5	2·6	3·2
		Maxilla M_1	Maxilla M_2	Maxilla M_3
Control 16 months	20	2·0	1·9	4·7
PD 1 year	5	1·5	1·9	11·5
PD 2 years	5	1·3	1·9	3·5

Table 8. *Length of premolar segment (mm)*

Group	Number of animals	Mandible (S.D.)	Maxilla (S.D.)
Control 1 year	5	74·2 (7·0)	63·9 (4·8)
PD 1 year	5	50·5 (2·8)	49·9 (3·3)
CD 1 year	5	38·9 (1·8)	39·4 (2·3)
Control 2 years	10	80·8 (7·3)	65·6 (4·1)
PD 2 years	5	58·5 (5·0)	55·8 (3·0)
CD 2 years	5	47·2 (4·0)	44·7 (4·4)

Tooth crowding

Table 8 shows that the amount of space available for the premolar teeth (Figs. 1, 2, *GH*) was reduced in both experimental groups, more so in the CD animals. The index used to express molar crowding has a value of unity when the teeth occupy a space precisely equal to the sum of their mesio-distal lengths. In the upper and lower jaws of one year old control pigs the index had a value of 0·99 (Table 9), indicating minimal crowding. Crowding was substantially increased in the experimental animals, being generally greater in the CD than in the PD group. It is noteworthy that between one and two years of age, molar crowding decreased in the PD, but increased in the CD animals.

Table 9. *Molar crowding index*

Group	Number of animals	Mandible (S.D.)	Maxilla (S.D.)
Control 1 year	5	0·99 (0·04)	0·99 (0·04)
PD 1 year	5	0·90 (0·05)	0·86 (0·07)
CD 1 year	5	0·88 (0·05)	0·91 (0·03)*
Control 2 years	9	0·98 (0·02)	0·96 (0·01)
PD 2 years	5	0·94 (0·02)	0·93 (0·02)
CD 2 years	5	0·84 (0·06)	0·73 (0·17)

* Based on M_1 and M_2 only.

DISCUSSION

All the malnourished animals lacked protein, but the PD animals were in a position to use more of their dietary protein for growth because more fat and sugar were available for energy production. It is not surprising therefore that the PD animals grew to be heavier and larger than the CD ones, and that there were differences in the sizes of the jaws and teeth in the two groups.

Examination of the lower jaw dimensions of the PD and CD animals showed that both the size and shape of the mandible were substantially affected. In both groups the height of the ascending ramus was reduced to a greater extent than the length of the body (Table 1), a point noted by Tonge & McCance (1965); similarly, the height of the ramus was more severely affected than its anteroposterior width (Table 2). Both these relative reductions were more pronounced in the CD than in the PD pigs. The reduction in height of the ascending ramus probably explains the observation of Tonge & McCance (1973) that the unerupted third molar appears to be situated in an abnormally 'high' position in the ascending ramus of CD pigs.

The disproportionate growth of the body of the mandible and the ascending ramus may be explained by (i) the anterior alveolar process and lower incisor teeth becoming more proclined (Table 3), effectively lengthening the body of the mandible, and (ii) the growth of the ascending ramus depending more on the growth rate of the condylar cartilage than on surface remodelling. Long bones of starved animals are severely reduced in length, more so than the jaws (Tonge & McCance, 1965), suggesting that proliferation of growing cartilage is more severely affected by starvation than is surface remodelling. In this respect, the finding that the length of the upper jaw and the length of the mandible were affected to almost the same extent in both experimental groups (Table 4) is consistent with the importance of surface remodelling in both jaws. Differences in the responses of cartilage and bone to dietary restrictions were also noted by Acheson (1959), who found that starvation reduced the thickness of the cartilage growth plate of the long bones of rats. This effect of starvation on chondrogenesis is probably mediated by hormonal changes, principally through a reduction in the activity of the pituitary gland (Vollmer, 1943). Although growth hormone itself does not appear to affect the growth of cartilage directly, it stimulates the liver to produce somatomedin, and this has been shown to increase proliferation of epiphyseal chondrocytes (Francis, Hill, Ash & Dehnel, 1975).

McCance, Ford & Brown (1961) found that the lower jaws of malnourished pigs were slightly less reduced in anteroposterior length than the upper jaws, and they attributed this to excessive growth at the condyle. The present results, however, not only indicate that this interpretation was erroneous, but also suggest that the slight difference in jaw growth which they noted was in fact due to increased proclination of the labial alveolar segment in the lower jaw.

In the pig, the final size of the first permanent molar crown is established shortly after birth (Tonge & McCance, 1973), and consequently its size was unaffected by malnutrition after birth (Table 5). The second molar was only slightly diminished by malnutrition, but the third permanent molar, the crown of which developed and grew throughout the period of malnutrition, was markedly reduced in size, especially in the CD pigs. Clearly, the rate and timing of tooth development were also retarded by malnutrition, for, in the maxilla, the third molar was not visible radiographically in one year old CD pigs when the corresponding tooth in control animals had reached 36 mm in mesio-distal diameter Nevertheless, even in the severely undernourished CD group, the maxillary third molar at two years of age reached 57 % of the size attained in controls, a figure inviting comparison with that of the upper jaw length which, in the same group, reached only 47 % of the size attained in well-fed animals. The maxillary third molar therefore suffered considerably less than the upper jaw, which was already some 80 mm long when the period of calorie dificiency began, whereas the third molar was just beginning to develop. Owens (1968) reported that the upper third molar of pigs was less affected by malnutrition than the lower third molar. The present study does not confirm this finding for, in both PD and CD pigs, the size of the upper third molar was reduced to a greater extent than that in the lower jaws. For example, in the two years old PD group, the diameter of the mandibular third molar was 83 % of that in control animals, whereas the corresponding figure for the maxillary third molar was 81 %. This difference was more pronounced in the two years old CD pigs, where the mandibular molar was 67 % of that in control animals but the maxillary tooth reached only 57 % of the size of the controls. Of course these differences may be partly due to the radiographic method employed: the restricted space for third molars in the small jaws of malnourished pigs forces them to rotate, and they will therefore be foreshortened in radiographs. Although both jaws were reduced to a similar extent in the experimental animals, space may have been more restricted for the upper than for the lower third molars because the latter could utilise the ascending ramus of the mandible. Upper third molars may therefore have been more foreshortened than lower third molars.

Clearly, tooth size can be reduced as a result of malnutrition, provided that the period of malnutrition occurs when the tooth is developing. The possibility of this happening on a large scale is limited because, in the pig (as in man), most tooth germs develop and grow at very early stages, so that they escape the effects of malnutrition imposed after birth. Deciduous teeth especially are protected by their early development, a point confirmed by Luke (1976), who found that in growth-retarded human fetuses the deciduous molars were not significantly smaller than those of a control group. Nevertheless, there is some indirect evidence that variations in human nutrition, although much less extreme than can be imposed upon experimental animals, may affect tooth size, for this is one explanation of the findings of Goose (1967) that the teeth of present-day children tend to be larger than those of their parents.

In well-fed one and two years old pigs, contralateral tooth asymmetry was greater in the first and third molars than in the second molar (Table 7). However, in these animals, the asymmetry of the first molar was very likely a result of attrition rather than a real variation in size, because the first molars of the PD animals (where the amount of attrition was probably less than in the controls) showed less contralateral asymmetry. In the PD group, asymmetry was greatest in the third molar and least in the first molar. This pattern of asymmetry is consistent with observations from studies of human teeth. For example, Garn, Lewis & Kerewsky (1965) demonstrated that, in man, the more mesial teeth of a morphological class show greater intercorrelations of size than do the more distal teeth of that class. This greater variability of distal as compared with mesial teeth of a particular class occurs not only in size but also in form (Sofaer, MacLean & Bailit, 1972). Furthermore, it is known that variability increases as nutritional conditions deteriorate, contralateral tooth asymmetry being higher, for example, in the natives of Tristan da Cunha than in the inhabitants of Boston, U.S.A. (Bailit, Workman, Niswander & MacLean, 1970). However, in the present study, contralateral asymmetry of the third molar apparently increased in the first year and then decreased between the first and second years of protein deficiency. Perhaps some biological advantage is gained if bilateral structures can develop and grow at different rates while nutritional conditions are poor, as this would increase the chances of at least one, and possibly both, reaching a functionally adequate size.

The quantitative estimates of tooth crowding confirmed previous qualitative observations on calorie deficient pigs (McCance, Owens & Tonge, 1968). Not only was the premolar alveolar segment considerably shortened at the expense of the post-canine diastema (Table 8), but molar crowding was also increased in both groups of malnourished animals (Table 9). The advantages for tooth accommodation of supplementing the calorie deficient diet with sugar or fat are shown by the reduction in molar crowding between one and two years in the PD group as compared with the CD animals.

In this study, the dietary regimes imposed upon the piglets were chosen to mimic those which are thought to cause kwashiorkor (protein deficiency) and marasmus (calorie deficiency) in man. The results may not only be applicable to severely malnourished children, but also to children in 'developed' countries whose general growth may be significantly retarded by long-term deficiencies in calorie intake (Davis, Apley, Fill & Grimaldi, 1978). Few detailed studies have been undertaken of the effects of malnutrition on the growth of the jaws and teeth in man, but one report (Parker, Dreizen & Spies, 1952) does suggest that variations of food intake in American children from different social groups may be associated with differences in craniofacial form. Further human studies are now needed to complement these derived from animal experimentation.

SUMMARY

Weanling pigs were separated into three groups: control animals were allowed unlimited food; protein deficient animals were allowed unlimited carbohydrate or fat but restricted in protein intake; calorie deficient animals were restricted in total food intake. The skulls and teeth of animals killed at one year and at two years of age were measured from radiographs, and from the results were derived the following conclusions:

(1) Pigs fed on protein and on calorie deficient diets all showed considerable retardation of the growth of jaws and teeth, consistently more severe in the calorie deficient than in the protein deficient animals.

(2) The shape of the mandible was altered by both types of malnutrition, the

height of the ascending ramus being reduced to a greater extent than either its anteroposterior width or the length of the body of the mandible. The labial alveolar process became more proclined with increasingly severe malnutrition.

(3) The upper and lower jaws were retarded to a similar extent in both groups of experimentally malnourished animals.

(4) Retardation of tooth growth was less severe than that of jaw growth.

(5) Contralateral asymmetry of molar crown size in the protein deficient animals was initially quite marked, but when the teeth were approaching their final size the asymmetry was no greater than in control animals.

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